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Cestoda from Lake Fishes in Wisconsin: The Ecology of *Proteocephalus ambloplitis* and *Haplobothrium globuliforme* in Bass and Bowfin

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ABSTRACT: Findings on *Proteocephalus ambloplitis* (Leidy) from bass in 2 southeastern Wisconsin eutrophic lakes show the importance of critical temperatures and host size in the parenteric recruitment of this tapeworm during the spring. The effect of latitudinal differences in the seasonal development of *P. ambloplitis* in southeastern Wisconsin compared with collections from elsewhere in North America are also noted. Enteric worms survived for up to 8 mo but lived and reproduced for longer periods in bowfin (*Amia calva*) in which recruitment was only dependent on the ingestion of plerocercoid-infected fish intermediate hosts. In southeastern Wisconsin, bowfin appeared to be the important host in which the majority of the *P. ambloplitis* population circulates. The tapeworm's initial establishment, maturation, and reproduction occurred in anteriormost digestive tract locations in both bass and bowfin. Establishment of *Haplobothrium globuliforme* Cooper, 1914 occurs anteriorly in bowfin, but adult and gravid worms are found only in the large intestine during peak breeding in the summer. Adults live up to 1 yr in the gut of bowfin. The mud minnow (*Umbra limi*) is a new intermediate host for *H. globuliforme* plerocercoids. The 2 tapeworm species had considerably denser populations in the closed system of Silver Lake than in the larger river-connected Tichigan Lake. The seasonal development of both *P. ambloplitis* and *H. globuliforme* in bowfin is reported here for the first time. Notes on concurrent infections with acanthocephalans, other *Proteocephalus* species, and hyperparasitism are also included.

KEY WORDS: Cestoda, *Proteocephalus ambloplitis, Proteocephalus* spp., *Haplobothrium globuliforme,* seasonal ecology, recruitment, infectious cycle, site selection, bass, bowfin, Wisconsin, concurrent infections, hyperparasitism.

The role of 16 fish species in the ecology of *Proteocephalus ambloplitis* (Leidy) plerocercoids in 2 southeastern Wisconsin eutrophic lakes was reported by Amin (1990). In the same 2 lakes, adults of this cestode species infect largemouth bass, *Micropterus salmoides* (Lacépède), and smallmouth bass, *M. dolomieui* Lacépède, as well as bowfin, *Amia calva* Linnaeus, which is also infected with *Haplobothrium globuliforme* Cooper, 1914. The ecological relationships among these organisms in southeastern Wisconsin are herein reported against a background that lacks any such information on *H. globuliforme* but involves various interpretations of some basic developmental and ecological phenomena unique to *P. ambloplitis* known only from bass.

Cooper (1914, 1917) described *H. globuliforme* and the fragmentation of its primary scolex. The study of the life history of this ancient and intriguing cestode was initiated by Essex (1929) and Thomas (1930) but was completed by Meinkoth (1947), based on material from Michigan. The most recent work on *H. globuliforme* is descriptive in nature, particularly at the ultrastructural level, e.g., MacKinnon and Burt (1985a, b, c). This tapeworm infects only *A. calva,* an ancient fish itself, throughout the United States and southern Canada. *Proteocephalus ambloplitis* has a similar distribution range. Cooper (1915, 1918) and Bangham (1927) provided early descriptions of the life history of the bass tapeworm, which was more completely investigated by Hunter (1928) and Hunter and Hunter (1929). Freeman (1973) and Fischer and Freeman (1969, 1973), however, provided the first complete account of its life history and the actual role of plerocercoids in bass from Ontario. Subsequently, the Ontario reference line was used to compare findings on the same cestode species from Michigan and South Carolina bass by Esch et al. (1975) and Eure (1976), respectively. Related findings from Wisconsin bass are described and compared, and those from bowfin are reported for the first time. The ecology of *H. globuliforme* in its only host, bowfin, is also reported here for the first time.

Materials and Methods

The fishes examined were from Silver Lake (Kenosha County), a 188-ha eutrophic land-locked lake, and from Tichigan Lake (Racine County), a 458-ha lake in an advanced state of eutrophication on the Fox River (a tributary of the Mississippi River). Seasonal collections were made from both lakes during the spring (April), summer (June, July, and early August), and

Table 1. Prevalence and intensity of *Proteocephalus ambloplitis* and *Haplobothrium globuliforme* in fishes of Silver and Tichigan lakes proper, 1976–1979.

			Silver Lake					Tichigan Lake				
			Fish		Cestodes			Fish		Cestodes		
Cestode species	Fish species	Season	*N*	Inf. (%)	*N*	$\bar{x}$/fish	Max.	*N*	Inf. (%)	*N*	$\bar{x}$/fish	Max.
Proteocephalus ambloplitis	*Amia calva*	Spring	7	7 (100)	845	120.7	372	13	12 (92)	619	47.6	195
		Summer	8	6 (75)	757	94.6	451	5	5 (100)	218	43.6	112
		Autumn	3	3 (100)	88	29.3	40	5	4 (80)	225	45.0	112
		Total	18	16 (89)	1,690	93.8	451	23	21 (91)	1,062	46.17	195
	Micropterus salmoides	Spring	28	26 (93)	543	19.4	86	2	0	0	—	0
		Summer	38	13 (34)	67	1.8	37	19	1 (5)	2	0.1	2
		Autumn	6	1 (17)	7	1.2	7	23	5 (22)	8	0.4	2
		Total	72	40 (56)	617	8.57	86	44	6 (14)	10	0.27	2
	Micropterus dolomieui	Spring	2	2 (100)	9	4.5	6	6	0	0	—	0
		Summer	2	0	0	—	0	10	0	0	—	0
		Autumn	0	0	0	—	0	2	0	0	—	0
		Total	4	2 (50)	9	2.25	6	18	0	0	0	0
Haplobothrium globuliforme	*Amia calva*	Spring	7	2 (29)	149	21.2	127	13	2 (15)	42	3.2	41
		Summer	8	6 (75)	305	38.1	94	5	4 (80)	62	12.4	41
		Autumn	3	1 (33)	117	39.0	117	5	2 (40)	4	0.8	3
		Total	18	9 (50)	571	31.7	127	23	8 (35)	108	4.70	41

Table 2. The relationship between the size and sex of *Micropterus salmoides* and *M. dolomieui* from Silver and Tichigan lakes and infection with *Proteocephalus ambloplitis*, 1976–1979.

Fish species	Lake	Fish total length (cm)	No. of male fish		*Proteocephalus ambloplitis*				No. of female fish	
						$\bar{x}$ per				
			Exam.	Inf. (%)	*N*	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)
Micropterus salmoides	Silver	11–20	2	2 (100)	10	5.0	5.0	7	5	0 (0)
		21–30	16	7 (41)	15	0.9	2.1	4	10	6 (60)
		31–40	11	4 (36)	41	3.7	10.2	18	17	10 (59)
		41–50	0	0	0	—	—	0	11	11 (100)
Totals			29	13 (45)	66	2.3	5.1	18	43	27 (63)
	Tichigan	11–20	6	0 (0)	0	—	—	0	5	0 (0)
		21–30	6	1 (17)	1	0.2	1.0	1	12	2 (17)
		31–40	4	0 (0)	0	—	—	0	8	1 (12)
		41–50	0	0	0	—	—	0	3	2 (67)
Totals			16	1 (6)	1	0.01	1.0	1	28	5 (18)
Micropterus dolomieui	Tichigan	18–20	3	1 (33)	4	1.3	4.0	4	0	0
		28	1	1 (100)	5	5.0	5.0	5	0	0
Totals			4	2 (50)	9	2.25	4.50	5	0	0

autumn (late October and November) between 1977 and 1979 and from Silver Lake during the summer of 1976. One thousand eight hundred twelve fishes representing 32 species and 10 families (Amiidae, 1 species; Catostomidae, 7; Centrarchidae, 9; Cyprinidae, 2; Esocidae, 2; Ictaluridae, 4; Lepisosteidae, 1; Percidae, 2; Salmonidae, 2; Serranidae, 2) were captured by electroshocking from both lakes. An additional 1,543 fishes representing 29 species and 11 families (Amiidae, 1; Catostomidae, 3; Centrarchidae, 6; Cyprinidae, 5; Cyprinodontidae, 2; Esocidae, 2; Gasterosteidae, 1; Ictaluridae, 4; Percidae, 3; Serranidae, 1; Umbridae, 1) were seined or minnow trapped in a channel draining the swampy western area of Tichigan Lake during 1978, 1979, and 1981.

Fish were systematically dissected shortly after capture. Specimens of parasites were processed as in Amin (1986a). The plerocercoid terminology of Freeman (1973) and Fischer and Freeman (1973) is used here. Representative specimens were deposited in the U.S. National Museum Helminthological Collection (USNM Helm. Coll.) and in the University of Nebraska State Museum's Harold W. Manter Laboratory Collection (HWML Coll.).

Results and Discussion

Host distribution

Prevalence and mean intensity of infections with *P. ambloplitis* were considerably greater in *A. calva* (89%, 93.9) than in either *M. salmoides* (56%, 8.6) or *M. dolomieui* (50%, 2.2) from Silver Lake. This pattern was consistent and more extreme than in Tichigan Lake, where infections were considerably lighter (Table 1). It is clear that the bowfin plays a major role in the flow of the *P. ambloplitis* suprapopulation in its fish definitive hosts in southeastern Wisconsin; see Amin (1987) for a discussion of host role changes. Parenteric recruitment of middle plerocercoid II into the bass gut, particularly in smallmouth bass, as originally described by Fischer and Freeman (1969) is not relevant to infections in bowfin. The cycle of *P. ambloplitis* in southeastern Wisconsin was clearly influenced by bowfin predation on plerocercoid-infected fish intermediate hosts, e.g., bowfin are not intermediate hosts of *P. ambloplitis* (see Amin, 1990). Accordingly, the "critical" spring temperatures of 7–12°C necessary for parenteric recruitment in bass (up from 4°C in Ontario and Michigan [Fischer and Freeman, 1969; Esch et al., 1975] and down from 26°C in South Carolina [Eure, 1976]) is not relevant to bowfin. This may explain why infection parameters of bowfin in the large river-connected Tichigan Lake were similar in all seasons (Table 1). Parameters in bowfin from the smaller landlocked Silver Lake, which shows greater fluctuations in seasonal temperature, were probably indicative of the higher intensity of fish feeding during spring and summer compared with autumn (Table 1).

Lake distribution

Both tapeworms (Table 1) had larger populations in Silver Lake than in Tichigan Lake, as noted earlier for *P. ambloplitis* plerocercoids (Amin, 1990), caryophyllaeid cestodes (Amin, 1986a), and some acanthocephalan species (Amin, 1986b). The closed system in the landlocked Silver Lake clearly enhanced the popu-

Table 2. Continued.

Proteocephalus ambloplitis				Total no. of fish		Proteocephalus ambloplitis			
	$\bar{x}$ per						$\bar{x}$ per		
N	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)	N	Exam. fish	Inf. fish	Max.
0	–	–	0	7	2 (29)	10	1.4	5.0	7
89	8.9	14.8	81	26	13 (50)	104	4.0	8.0	81
303	17.8	30.3	86	28	14 (50)	344	12.3	24.6	86
159	14.5	14.5	32	11	11 (100)	159	14.4	14.4	32
551	12.8	20.4	86	72	40 (56)	617	8.6	15.4	86
0	–	–	0	11	0 (0)	0	–	–	0
3	0.3	1.5	2	18	3 (17)	4	0.2	1.3	2
2	0.3	2.0	2	12	1 (8)	2	0.2	2.0	2
6	2.0	3.0	5	3	2 (67)	6	2.0	3.0	5
11	0.4	2.2	5	44	6 (14)	12	0.3	2.0	5
0	–	–	0	3	1 (33)	4	1.3	4.0	4
0	–	–	0	1	1 (100)	5	5.0	5.0	5
0	–	–	0	4	2 (50)	9	2.3	4.5	5

lation density of these helminths. Other variables related to the different state of eutrophication in the 2 lakes may include species composition, distribution and density of the intermediate hosts, and the feeding strategy of the definitive hosts involved. The lower visibility in Tichigan Lake could negatively affect feeding on infected prey by bass (a sight feeder) and contribute to the large difference in prevalence in the 2 lakes (Table 1). Feeding of the bottom-dwelling bowfin (probably an olfactory and tactile feeder) would not be strongly affected by decreased visibility.

Host size and sex

Two of 7 *M. salmoides* below 20.0 cm in total length (less than 2 yr old; see Pasch [1974]) from Silver Lake were lightly infected with enteric *P. ambloplitis*; none of 11 similar fishes from Tichigan Lake were infected. Heavier and more frequent infections were largely confined to mature larger bass (Table 2). The shift from a microcrustacean and insect diet to a fish diet in larger largemouth bass started in 5-cm long bass (Pasch, 1974, among others). It is not certain whether these data support the hormone factor hypothesis of Fischer and Freeman (1969) and Esch et al. (1975), who suggested that sex hormones of mature bass >15.0 and >20.0 cm in length, respectively, may affect the parenteric migration of middle plerocercoid II in the bass gut. The possible contribution of cannibalism to the abundance of enteric *P. ambloplitis* in bass in not known. In both lakes, female largemouth bass were considerably more heavily and more frequently infected than males (Table 2). Whether female sex hormones have greater effect than male hormones in promoting parenteric recruitment is not known. Fischer and Freeman (1969) indicated that proper rise in temperature and bass size (maturity), but "apparently" not bass sex, were important for penetration. The feeding behavior of male vs. female bass is not known.

In *A. calva,* the smallest fish examined were infected with *P. ambloplitis* (Table 3). Although virtually all bowfin were infected, larger fish from both lakes had heavier worm burdens, which would correspond with the larger volume of food (infected bass) eaten by these fish. Unlike the pattern in bass (Table 2), there appeared to be no marked difference in infection parameters by sex of *A. calva* (Table 3).

The pattern of *H. globuliforme* infection in *A. calva* (Table 4) was similar to that of *P. ambloplitis* from the same host (Table 3) except that the increase in *H. globuliforme* burden by fish size was smaller, whereas the difference between female and male host infection parameters was greater. The life history of *H. globuliforme* is similar to that of *P. ambloplitis* in *A. calva* but without the complication of the different types of plerocercoids. Bowfin appear to become infected by ingesting a second fish intermediate host, e.g., *Lepomis* or *Ictalurus* infected (with extraintestinal plerocercoids) from feeding on plerocercoid-infected copepods. The considerably greater intensity and higher prevalence of

Table 3. The relationship between the size and sex of *Amia calva* from Silver and Tichigan lakes and the intensity of infection with *Proteocephalus ambloplitis*, 1976–1979.

				Proteocephalus ambloplitis					
		No. of male fish			$\bar{x}$ per			No. of female fish	
Lake	Fish total length (cm)	Exam.	Inf. (%)	*N*	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)
Silver	20–29	0	0	0	—	—	0	55	55 (100)
	30–39	0	0	0	—	—	0	1	1 (100)
	40–49	2	2 (100)	241	120.5	120.5	159	1	1 (100)
	50–59	5	3 (60)	100	20.0	33.3	44	4	4 (100)
	60–69	0	0	0	—	—	0	0	0
Totals		7	5 (71)	341	48.7	68.2	159	11	11 (100)
Tichigan	20–29	1	1 (100)	63	63.0	63.0	63	0	0
	30–39	0	0	0	—	—	0	0	0
	40–49	2	2 (100)	4	2.0	2.0	3	3	2 (67)
	50–59	11	10 (91)	450	40.9	45.0	112	4	3 (75)
	60–69	0	0	0	—	—	0	2	2 (100)
Totals		14	13 (93)	517	36.9	39.8	112	9	7 (78)

* Nine of these hosts were also infected with *Haplobothrium globuliforme.*
† Eight of these hosts were also infected with *Haplobothrium globuliforme.*

infection in female than in male bowfin suggests a larger volume of food intake in females vs. males of the same size. This argument may also hold for bass.

Seasonal distribution

The distribution of *P. ambloplitis* in *M. salmoides* from Silver Lake shows peak prevalence and mean intensity in the spring (93%, 19.4), decreasing in the summer and autumn to 34%, 1.8, and 17%, 1.2, respectively; the number of worms from the same host in Tichigan Lake was much smaller (Table 1). Most of the spring tapeworms were recently recruited immatures (7% plerocercoids and 78% juveniles) (Table 5) that must have reached enteric sites during April and May, and possibly earlier. Some recently recruited plerocercoids in bass and bowfin were considerably smaller (occasionally little more than a scolex) than many of those infecting body cavity organs (particularly ovaries) of fish intermediate hosts (Amin, 1990). The summer worms included a considerably higher proportion of mature adults (58%) and gravid adults (8%), which

Table 4. The relationship between the size and sex of *Amia calva* from Silver and Tichigan lakes and the intensity of infection with *Haplobothrium globuliforme*, 1976–1979.

				Haplobothrium globuliforme					
		No. of male fish			$\bar{x}$ per			No. of female fish	
Lake	Fish total length (cm)	Exam.	Inf. (%)	*N*	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)
Silver	20–29	0	0	0	—	—	0	5	3 (60)
	30–39	0	0	0	—	—	0	1	1 (100)
	40–49	2	0	0	—	—	0	1	1 (100)
	50–59	5	0	0	—	—	0	4	4 (100)
	60–69	0	0	0	—	—	0	0	0
Totals		7	0	0	—	—	0	11	9 (82)
Tichigan	20–29	1	1 (100)	1	1.0	1.0	1	0	0
	30–39	0	0	0	—	—	0	0	0
	40–49	2	0	0	—	—	0	3	2 (67)
	50–59	11	1 (9)	3	0.3	3.0	3	4	2 (50)
	60–69	0	0	0	—	—	0	2	2 (100)
Totals		14	2 (14)	4	0.3	2.0	3	9	6 (67)

* All these hosts were also infected with *Proteocephalus ambloplitis.*

Table 3. Continued.

Proteocephalus ambloplitis				Total no. of fish		Proteocephalus ambloplitis			
	$\bar{x}$ per						$\bar{x}$ per		
N	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)	*N*	Exam. fish	Inf. fish	Max.
127	25.4	25.4	54	5	5 (100)	127	25.4	25.4	54
372	372.0	372.0	372	1	1 (100)	372	372.0	372.0	372
451	451.0	451.0	451	3	3 (100)	692	230.7	230.7	451
399	99.8	99.8	132	9	7 (78)	499	55.4	71.3	132
0	—	—	0	0	0	0	—	—	0
1,349	122.6	122.6	451	18*	16 (89)	1,690	93.9	105.6	451
0	—	—	0	1	1 (100)	63	63.0	63.0	63
0	—	—	0	0	0	0	—	—	0
114	38.0	57.0	112	5	4 (80)	118	23.6	29.5	112
50	12.5	16.7	27	15	14 (93)	651	43.4	46.5	151
230	115.0	115.0	195	2	2 (100)	230	115.0	115.0	195
394	43.8	56.3	195	23†	21‡ (91)	1,062	46.2‡	50.6‡	195

‡ One 57-cm-long fish was not sexed. It contained 151 worms. This fish and its parasites were included in the totals but not under either male or female columns.

disappeared from the dwindling autumn population in October and November. The above findings suggest a major recruitment (possibly mostly parenteric) beginning in late March and extending at least through June (25% of summer material were juveniles, Table 5). Maturation proceeded sufficiently fast to produce breeding gravid adults in the summer. By autumn most worms had already disappeared, leaving only 7 adults in 1 out of 6 bass examined. Mature adults of the autumn were considerably smaller than the more robust ones of the summer. Clearly there is no reason to suspect winter *P. ambloplitis* in the gut of *M. salmoides.* The few data from *M. dolomieui* (Tables 1, 5) fit the pattern described in *M. salmoides.* Findings from bass thus suggest an enteric *P. ambloplitis* life span of no more than 8 mo in southeastern Wisconsin, which may be a few weeks longer than that of the same tapeworm species in *M. dolomieui* reported in more northern locations, e.g., Fischer and Freeman (1969) and Esch et al. (1975) from Ontario and Michigan, respectively. Temperature gradient was probably involved in this latitudinal

Table 4. Continued.

Haplobothrium globuliforme				Total no. of fish		Haplobothrium globuliforme			
	$\bar{x}$ per						$\bar{x}$ per		
N	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)	*N*	Exam. fish	Inf. fish	Max.
123	24.6	41.0	51	5	3 (60)	123	24.6	41.0	51
22	22.0	22.0	22	1	1 (100)	22	22.0	22.0	22
94	94.0	94.0	94	3	1 (33)	94	31.3	94.0	94
332	83.0	83.0	127	9	4 (44)	332	37.0	83.0	127
0	—	—	0	0	0	0	—	—	0
571	51.9	63.4	127	18	9* (50)	571	31.7	63.4	12
0	—	—	0	1	1 (100)	1	1.0	1.0	1
0	—	—	0	0	0	0	—	—	0
9	3.0	4.5	8	5	2 (40)	9	1.8	4.5	8
43	10.8	21.5	41	15	3 (20)	46	3.1	15.3	41
52	26.0	26.0	41	2	2 (100)	52	26.0	26.0	41
104	11.6	17.3	41	23	8* (35)	108	4.7	13.5	41

variation. In all other respects, our results from Wisconsin are in agreement with those of the above authors and are thus supportive of the critical temperature of parenteric recruitment in bass. The longer life span of parenteric *P. amblopliti*s plerocercoids in bass or other species of fish intermediate hosts (Amin, 1990) classes *P. ambloplitis* among the semelparous brevipatent one-time seasonal breeders with short adult life span (in bass); see Kennedy (1983). The increase in intensity of *P. ambloplitis* plerocercoids in older *Lepomis macrochirus* body cavity locations was interpreted by Bailey (1984) as reflecting plerocercoid longevity. Bailey's (1984) observation may also express an increased probability of exposure due to greater food intake by large fish. The seasonal maturation in this type of life history is clearly timed to coincide with the optimal period for transmission when plankton are most abundant. Seasonality may thus be more effectively determined at the level of the intermediate host, its seasonal and spatial availability, and dormancy.

The seasonal pattern of tapeworm infection in bowfin adds a new dimension to the developmental aspects of *P. ambloplitis* population ecology that is of major importance because *A. calva* appears to be the major definitive host in southeastern Wisconsin (Table 1). The parenteric recruitment and its associated critical spring temperatures as well as the potential hormonal factor excluding recruitment in immature bass are not parts of the bowfin biological system (see Host distribution, Host size and sex, above). The most important remaining variable is the feeding behavior. The prevalence of *P. ambloplitis* in *A. calva* from both lakes as well as the mean intensity of infection in Tichigan Lake showed no seasonal differences. The mean intensity in Silver Lake was, however, lower in the autumn, probably reflecting less feeding activity (Table 1). The smaller land-locked Silver Lake probably shows more extremes of seasonal temperatures. In that lake, the proportion of mature worms in bowfin in the spring (37%) was considerably higher than in largemouth bass (15%), was stable through the summer (38%), and peaked in the autumn (83%) (Table 5). Freshly recruited plerocercoids and juveniles as well as gravid worms were also represented in the autumn. These conditions were even more pronounced in Tichigan Lake where 84% of the spring worms were mature (3 specimens were gravid) and 16% of the autumn specimens were gravid. It is clear from the above findings, and in the absence of the constraints operating on bass, that the recruitment season in bowfin must begin well before April, with egg laying extending well past November. This significantly increases the length of the breeding season of *P. ambloplitis* in *A. calva* and thus increases its reproductive potential. It is interesting to come across 2 such different reproductive strategies of the same tapeworm infecting 2 genera of fish definitive hosts in the same body of water.

Infection parameters of *H. globuliforme* in *A. calva* were more or less seasonally stable in Silver Lake but were less consistent in Tichigan Lake (Table 1). Like *P. ambloplitis* in bowfin, the life cycle of *H. globuliforme* involves a copepod and fish intermediate hosts whose distribution and seasonal availability may differ in both lakes. Recently recruited *H. globuliforme* juveniles were represented in all collections from both lakes, but in Silver Lake, a high proportion (41%) was present during the spring, suggesting more active recruitment then. Primary scolices were found only on about one-half of the juvenile worms; the rest of the juveniles and all other stages had only secondary scolices (Table 6). Worms with primary scolices were clearly the youngest and represented the earliest recruitments. MacKinnon and Burt (1985c) also observed a higher proportion of *H. globuliforme* collected from *A. calva* in Lake Ontario in late June than in late August. In Silver Lake, maturation and breeding increased during the warmer months from 36% mature and 19% gravid in the spring to 33% and 37% in the summer; no gravid worms were recovered during the autumn but recruitment continued (Table 6). Worms matured more rapidly in Tichigan Lake, but both mature and gravid worms disappeared by October. The above observations and the lighter autumn infections, particularly in Tichigan Lake, suggest the absence of *H. globuliforme* from bowfin during the winter.

Twenty-four *H. globuliforme* plerocercoids were recovered from the body cavity of 19 of 66 (29%) mud minnows, *Umbra limi* (Kirtland), examined from Tichigan Lake canal during the summer. Most of these were excysted from double-walled cysts. The outer cyst wall appeared to be of host origin—a new observation. The plerocercoids resembled the pyriform ones reported by Meinkoth (1947, Fig. 1) from the liver of

Table 5. Seasonal development of *Proteocephalus ambloplitis* in fishes from Silver and Tichigan lakes, 1976–1979.

		Spring (Apr)					Summer (Jun–early Aug)					Autumn (late Oct, Nov)				
Lake	Fish species	*N*	Plero-cercoids* (%)	Juveniles† (%)	Mature (%)	Gravid (%)	*N*	Plero-cercoids (%)	Juveniles (%)	Mature (%)	Gravid (%)	*N*	Plero-cercoids (%)	Juveniles (%)	Mature (%)	Gravid (%)
Silver	*Amia calva*	845	461 (54)	73 (9)	311 (37)	0	757	248 (33)	190 (25)	291 (38)	28 (4)	88	2 (2)	9 (10)	73 (83)	4 (5)
	Micropterus salmoides	543	40 (7)	424 (78)	79 (15)	0	67	17 (25)	6 (9)	39 (58)	5 (8)	7	0	0	7 (100)	0
	Micropterus dolomieui	9	6 (67)	0	3 (33)	0	0	0	0	0	0	0	0	0	0	0
Total		1,397	507 (36)	497 (36)	393 (28)	0	824	265 (32)	196 (24)	330 (40)	33 (4)	95	2 (2)	9 (10)	80 (84)	4 (4)
Tichigan	*Amia calva*	619	25 (4)	70 (11)	521 (84)	3 (1)	218	3 (1)	19 (9)	144 (66)	52 (24)	225	21 (9)	26 (12)	140 (62)	38 (17)
	Micropterus salmoides	0	0	0	0	0	2	0	0	0	2 (100)	8	0	1 (13)	7 (87)	0
Total		619	25 (4)	70 (11)	521 (84)	3 (1)	220	3 (1)	19 (9)	144 (65)	54 (25)	233	21 (9)	27 (12)	147 (63)	38 (16)

* Terminal plerocercoids.
† Segmented but still small and sexually immature.

Table 6. Seasonal development of *Haplobothrium globuliforme* in *Amia calva* of Silver and Tichigan lakes, 1976–1979.

	Spring (Apr)						Summer (Jun–early Aug)						Autumn (late Oct, Nov)					
Lake	*N*	Juv. 1* (%)	Juv. 2† (%)	Young‡ (%)	Mature (%)	Gravid (%)	*N*	Juv. 1 (%)	Juv. 2 (%)	Young (%)	Mature (%)	Gravid (%)	*N*	Juv. 1 (%)	Juv. 2 (%)	Young (%)	Mature (%)	Gravid (%)
Silver	149	29 (19)	32 (22)	6 (4)	54 (36)	28 (19)	305	39 (13)	8 (3)	44 (14)	102 (33)	112 (37)	117	17 (15)	11 (9)	32 (27)	57 (49)	0
Tichigan	42	2 (5)	0	9 (21)	20 (48)	11 (26)	62	4 (7)	0	2 (3)	18 (29)	38 (61)	4	4 (100)	0	0	0	0

* Juveniles with primary scolex.
† Juveniles with secondary scolex.
‡ Larger worms but still without sexually mature segments.

Table 7. Seasonal site selection of *Haplobothrium globuliforme* in *Amia calva* and *Proteocephalus ambloplitis* in *Amia calva*, *Micropterus salmoides*, and *Micropterus dolomieui* from Silver and Tichigan lakes, 1976–1979.

			Spring (Apr) (%)*							
Cestode	Host species	Lake	*N*	A†	Ce	B1	B2	C1	C2	C3
Haplobothrium globuliforme	*Amia calva*	Silver	149	—	—	1.3	—	23.5	33.6	41.6
		Tichigan	42	—	—	—	—	83.3	14.3	2.4
Proteocephalus ambloplitis	*Amia calva*	Silver	845	49.1	—	41.9	1.3	6.9	0.2	0.6
		Tichigan	619	26.0	—	38.9	—	33.6	0.5	1.0
	Micropterus salmoides	Silver	543	38.3	38.7	11.4	6.6	1.9	3.1	—
		Tichigan	—	—	—	—	—	—	—	—
	Micropterus dolomieui	Silver	9	33.3	11.1	55.6	—	—	—	—
		Tichigan	—	—	—	—	—	—	—	—

* % of worms in intestinal regions.

† A: stomach; Ce: cecum; B1, B2: small intestine; C1–C3: large intestine. (*Amia calva* has no cecum and *Micropterus* has no C3.)

guppies, *Poecilia reticulata* Peters. The Wisconsin specimens, however, were more elongate with a distinct long cylindrical neck and a bladder that was either abruptly spheroidal (in 1 specimen) or gradually enlarged distally. *Umbra limi* is a new intermediate host for *H. globuliforme*.

Seasonal site selection

Data from Table 7 show anteriormost localization of *H. globuliforme* during the summer. During the summer, stomach (A) and small intestine (B1, B2) were occupied by 9.2, 32.1, and 36.7% of worms, respectively (Table 7). Quick posterior migration would clearly reduce competition with *P. ambloplitis*, which usually occupy anterior locations. Regions A and B in *A. calva* were practically free of *H. globuliforme* infections during autumn and spring.

Site selection of *P. ambloplitis* in *A. calva* did not show any particular seasonal predeliction. The anteriormost gut regions (A, B1) appear to be the optimum sites for maturation and breeding, as they are for initial establishment of *P. ambloplitis* in *A. calva* during all seasons.

In bass, different forces appear to be involved in the seasonal site selection of *P. ambloplitis*. Here the major parenteric recruitment occurred largely during the spring, but most of the worms from Silver Lake (the larger sample) were in the stomach (38.3%) and the cecum (38.7%) (Table 7). The ceca of bass appear to be optimum for *P. ambloplitis* maturation and breeding. The stomach distribution appears to have been an artifact of regurgitation upon capture. Worms found in other intestinal locations (also from *M. dolomieui*) were mostly enteric plerocercoids (terminal-II) that must have just penetrated the gut wall.

Concurrent infections

Both species of *Micropterus* were also commonly infected with *Neoechinorhynchus cylindratus* (Van Cleave, 1913) Van Cleave, 1919 and *Leptorhynchoides thecatus* (Linton, 1891) Kostylev, 1924 (Acanthocephala) and less commonly with *Camallanus oxycephalus* Ward and Magath, 1916 (Nematoda) in both lakes. Rare infections with *Neoechinorhynchus prolixoides* Bullock, 1963 in both bass species were also noted from Silver Lake, and 1 largemouth bass from Tichigan Lake was infected with 1 *Pomphorhynchus bulbocolli* Linkins *in* Van Cleave, 1919 (Acanthocephala). The anterior position of both *P. ambloplitis* and *L. thecatus* did not show significant seasonal changes, whereas *N. cylindratus* underwent marked posterior migration between autumn and summer (see Amin [1986b] for details).

Amia calva was also occasionally infected with the trematodes *Azygia longa* (Leidy, 1851) in both lakes, *A. angusticauda* (Stafford, 1904) Manter, 1926 in Tichigan Lake, and *Macroderoides spiniferus* Pearse, 1924 in Silver Lake. *Azygia* spp. primarily occupied the stomach, and *M. spiniferus* were confined to the posterior 75% of the gut (Amin, 1982).

Hyperparasitism

One adult *P. ambloplitis* in the cecum of a 36-cm-long male largemouth bass from Silver Lake examined during the spring was penetrated by a male *L. thecatus*. Similarly, a *P. ambloplitis* ple-

Table 7. Continued.

Summer (Jun–early Aug) (%)								Autumn (late Oct, Nov) (%)							
N	A	Ce	B1	B2	C1	C2	C3	*N*	A	Ce	B1	B2	C1	C2	C3
305	9.2	—	32.1	36.7	15.8	2.6	3.6	117	—	—	—	—	95.7	1.7	2.6
62	3.2	—	24.2	—	72.6	—	—	4	—	—	—	—	75.0	25.0	—
757	83.5	—	11.5	1.1	1.4	0.3	2.2	88	80.7	—	19.3	—	—	—	—
218	59.2	—	39.4	—	—	0.5	0.9	225	46.2	—	31.1	—	9.4	13.3	—
67	43.3	23.9	3.0	10.4	3.0	16.4	—	7	—	—	28.6	42.9	—	28.5	—
2	100.0	—	—	—	—	—	—	10	10.0	20.0	40.0	20.0	10.0	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

rocercoid in the liver of a 46-cm-long female largemouth bass from Tichigan Lake examined during the autumn was penetrated by a female *L. thecatus*. *Leptorhynchoides thecatus* occasionally passes into extraintestinal sites of centrarchids (Amin, unpubl.). Both incidents appear to be chance occurrences. Two other similar associations were previously reported by Miller (1946) of *Echinorhynchus salvelini* Schrank, 1788 (=*Pomphorhynchus laevis*) (Zoega *in* Müller, 1776) Van Cleave, 1924 attached to *Eubothrium salvelini* (Schrank, 1790) and by Muzzall and Rabalais (1975) of *Acanthocephalus jacksoni* Bullock, 1962 (=*A. dirus* (Van Cleave, 1931) Van Cleave and Townsend, 1936) attached to *Proteocephalus* sp. The first case was attributed to overcrowding and the second to chance occurrence.

Other helminths

A few individuals of at least 3 species of *Proteocephalus* Weinland, 1858 were found in the ceca and intestines of largemouth bass from both lakes. One species (1 mature individual 130 mm long) in a Silver Lake bass had 4 suckers, each with pointed apex, and a sizable vestigial fifth sucker in a broad anterior depression. Another species (6 immature worms 20–40 mm long) from Silver Lake had 4 large highly muscular suckers deeply set in an expanded bulbous scolex well set off from a long neck, with faint segmentation. A third species (7 immatures 1–3 mm long and 6 mature adults 9–23 mm long) from both lakes had a gradually expanded scolex with 4 ovoidly expanded suckers and a dome-shaped fifth, almost equally expanded and not much smaller. The juveniles and adults of this third species may actually belong to 2 different species. The above material was not sufficiently informative to assign satisfactory specific identifications. All specimens clearly only accidentally infected bass.

Conclusions

All work reported so far on the life history and development of *P. ambloplitis* since Cooper's (1918) earliest account has reported bass, *Micropterus* spp., as the definitive host. The more recent additions to Hunter's (1928) and Hunter and Hunter's (1929) scheme and the understanding of parenteric migration of plerocercoids by Fischer and Freeman (1969, 1973), Esch et al. (1975), and Eure (1976) were also based on studies of *M. dolomieui*. Records of bowfin as a host of adult *P. ambloplitis* were noted by Hoffman (1967). This study shows that bowfin, and not bass, is the major host of *P. ambloplitis* in southeastern Wisconsin This host specificity occurs in the presence of large populations of bass in the same waters. This is clearly a matter of more than "host role change" as explained by Amin (1987) and must involve a certain element of host preference. The role of other definitive hosts, e.g., *Morone chrysops* and *M. mississippiensis* (Arnold et al., 1968; McReynolds and Webster, 1980) in the biology of *P. ambloplitis* is not known.

Bowfin become infected by ingesting plerocercoid (middle-II)-infected fish intermediate hosts. Enteric *P. ambloplitis* has a longer life span and a longer breeding season in bowfin than in bass, even though it also seems to disappear during the winter. In bass, *P. ambloplitis* is present for

no more than 8 mo, with parenteric recruitment occurring mostly during the spring and possibly influenced by host size (sexual maturity), as has been reported in Ontario and Michigan by Fischer and Freeman (1969) and Esch et al. (1975), respectively. In these 2 locations, the life span of enteric *P. ambloplitis* appeared to be somewhat shorter than in Wisconsin bass (this study). Enteric infections in the winter (absent between September and November) were reported in South Carolina (Eure, 1976). The following factors thus appear to influence the seasonal development of *P. ambloplitis*: (1) temperature, (2) latitudinal differences, (3) host size (hormonal factors), and (4) host species. The first 3 factors were explored earlier (Fischer and Freeman, 1969; Esch et al., 1975; Eure, 1976) in bass and are, at least partially, supported by this study.

Initial establishment and maturation of *P. ambloplitis* appear to occur in the anteriormost locations of both bass and bowfin digestive tracts. These traits were not significantly seasonally variable. Although initial establishment of *H. globuliforme* appeared also to have occurred in the anteriormost gut locations of the bowfin, further development and breeding occurred exclusively in the large intestine. Metabolic requirements of maturation and reproduction as well as decreasing competition with *P. ambloplitis,* which consistently occupied anterior gut regions of this host, probably influenced the location of *H. globuliforme.* Recruitment of *H. globuliforme* in *A. calva,* like that of *P. ambloplitis,* depended on the ingestion of plerocercoid-infected fish intermediate hosts, involving at least *U. limi* in Tichigan Lake during the summer, with active reproduction occurring during the spring and peaking in the summer. Adult *H. globuliforme* appear to live in *A. calva* from recruitment of initial juveniles in spring and summer to gravid adults in the same summer. The seasonal ecology of *H. globuliforme* in its fish definitive host, *A. calva,* is reported here for the first time.

Both tapeworm species had larger population sizes in the smaller land-locked Silver Lake than in the larger river-connected Tichigan Lake. The difference in tapeworm distribution and prevalence between lakes may also have been related to differences in eutrophication levels affecting intermediate host population parameters and visibility as well as definitive host feeding strategies. The enhancement of population density of other helminth species in closed systems like Silver Lake has also been demonstrated (Amin, 1986a, b). Seasonal differences in temperature (more extreme in Silver Lake than in Tichigan Lake) appeared to have affected the feeding behavior and subsequently the recruitment of tapeworms, e.g., *P. ambloplitis,* by *A. calva.*

Of the relatively common helminth associates in bass, only *L. thecatus* shared anterior gut locations with *P. ambloplitis*; neither helminth showed significant seasonal changes in site selection. This clearly provided the opportunity for an accidental (opportunistic?) attachment of 1 *L. thecatus* to an individual *P. ambloplitis.*

Deposited Specimens

Haplobothrium globuliforme from *A. calva* from Tichigan Lake (USNM Helm. Coll. Nos. 80515–80518) and from Silver Lake (HWML Coll. Nos. 24913–24922). *Proteocephalus ambloplitis* from *A. calva* from Tichigan Lake (USNM Helm. Coll. Nos. 80519–80522) and from Silver Lake (HWML Coll. Nos. 24923–24933), and from *M. salmoides* from Tichigan Lake (USNM Helm. Coll. Nos. 80523–80525) and from Silver Lake (HWML Coll. Nos. 24934–24946).

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